

A PROTEROSUCHIAN THECODONT FROM THE REWAN FORMATION OF QUEENSLAND

RICHARD A. THULBORN
Department of Zoology, University of Queensland

ABSTRACT

A new proterosuchian reptile, *Kalisuchus rewanensis*, is described on the basis of fragmentary skull and postcranial remains from the Lower Triassic (Rewan Formation) of SE Queensland. The classification of proterosuchians is briefly reviewed and *Kalisuchus* is referred to the family Proterosuchidae on account of its many resemblances with Chinese and African species of *Chasmatosaurus* (*Proterosuchus* auct.). *Kalisuchus* was an amphibious and superficially crocodile-like predator that probably reached a maximum body length of two or three metres. Its relationships with other proterosuchians suggest that the parent sediments may be correlated with the upper part of the S. African *Lystrosaurus* Zone (or, possibly, with the lower part of the *Cynognathus* Zone). This tentative correlation is supported by palaeobotanical evidence. The Rewan vertebrate fauna may be interpreted as a Palaeozoic relict in order to account for its surprising lack of synapsid reptiles (notably *Lystrosaurus*).

The late Permian and early Triassic reptiles known as proterosuchians were probably the basal stock of the entire subclass Archosauria. They were, in other words, the remote ancestors of animals as varied as the crocodylians, the pterosaurs (or flying reptiles) and the two great groups of dinosaurs (saurischians and ornithischians). Remains of proterosuchians are known from South Africa, China, India, Russia, and possibly Argentina (see Charig and Sues 1976 for a comprehensive review). Despite their obvious importance for understanding of archosaur history the proterosuchians are still rather poorly known, most being represented by rare and fragmentary fossils. In such circumstances practically any new proterosuchian material will be of considerable interest.

This paper concerns a proterosuchian from the Rewan Formation of Queensland. While its remains are far from complete — in established proterosuchian tradition — they do nevertheless provide a good deal of significant new information, particularly with respect to dating of the Rewan Formation and to the relationship between proterosuchians and pseudosuchians. This proterosuchian is the earliest archosaur yet described from Australia.

MATERIAL

Most material comes from a single locality, known as the Crater, situated 72 km southwest of Rolleston and 11 km south of Rewan homestead.

The Crater is a steep-sided basin, some 200 m across, which cuts into red beds at about the middle part of the Rewan Formation. The exposed sediments are red, brown, and green silts and mudstones with occasional sandy layers and strings of ironstone nodules. These beds are probably of Lower Triassic age and were apparently laid down by a system of meandering streams (Howie 1972a). Most specimens are isolated bone fragments that had been washed down on to the floor of the Crater by rain; very few specimens were found in the walls of the basin. Many of the bone fragments have been shattered by crushing and by weathering, and some seem to have suffered transport before burial. The bone itself is grey, cream or white in colour, but is usually stained black, brown or red by iron.

A few specimens were collected from a second locality, Duckworth Creek, which is situated southwest of the settlement of Bluff and about 127 km north-northeast of the Crater. This locality has been described by Howie (1972b), who explained that the sediments exposed there may be correlated directly with those of the Crater. In its preservation and appearance the Duckworth Creek material is virtually identical with that from the Crater.

All illustrated specimens were collected from the Crater and have individual QM catalogue numbers (see captions); non-figured material is catalogued under K10125 (from the Crater) or F9549 (from Duckworth Creek).

SYSTEMATICS

Class REPTILIA

Subclass ARCHOSAURIA

Order THECODONTIA Owen 1859

Suborder PROTEROSUCHIA Broom 1906

Family PROTEROSUCHIDAE Broom 1906

Genus *Kalisuchus* gen. nov.

Type and only species *K. rewanensis* sp. nov.

Kalisuchus rewanensis sp. nov.

HOLOTYPE: single right maxilla, QM F8998 (Plate 1, figs. A–C; Plate 2, fig. A).

REFERRED MATERIAL: an assortment of bone fragments from skull, vertebral column, limb girdles and limbs (QM catalogue numbers under 'Material').

LOCALITIES: the Crater, Rewan property, about 72 km southwest of Rolleston, SE Queensland (field locality L78 in QM records); a small amount of referred material was obtained from Duckworth Creek, near Bluff, SE Queensland.

HORIZON: lower beds of the upper part of the Rewan Formation, Mimosa Group; Lower Triassic.

ETYMOLOGY: the genus is named for Kali, goddess of destruction, in allusion to suspected predatory habits of the animal; the specific name refers to provenance of material.

DIAGNOSIS (genus and species): proterosuchid thecodontian with narrow and lightly constructed skull. Orbit large, pear-shaped or triangular (narrower below), set higher than lateral temporal fenestra, with rugose ornament on upper rim. Snout laterally compressed, with transversely expanded and downcurved tip, and with large antorbital fenestra roofed by lacrimal. Palate narrow, with long slit-like internal nares flanked by flat medial faces of maxillae. Jugal with blade-like process on ventral rim and with posterior ramus shaped like an inverted L-girder in cross-section. Rear edge of postorbital set into deep slit in leading edge of dorsal jugal ramus. Mandible robust, deeper than wide anteriorly, with splenial extending forwards almost to the loose symphysis; jaw wide and shallow at suspensorium, with unfused prearticular in front of glenoid fossa, and with prominent and straight retroarticular process. Near-isodont dentition of compressed, recurved and acutely pointed teeth having finely serrated rear edges; implantation subthecodont; upper tooth row interrupted at

junction of maxilla and premaxilla. All centra spool-shaped, amphicoelous, longer than high and laterally compressed. Neck centra elongate, strongly keeled, perhaps with crescentic facets for small intercentra; trunk centra distinctly shorter than those of neck, weakly keeled or without keels; tail centra elongate, with weak paired keels or with smooth ventral surfaces. Neural spines of neck and trunk regions with dorsal edges swollen into very large spine tables. Posterior neck vertebrae with triple-headed ribs. Acetabulum imperforate; distal part of pubis twisted and transversely expanded. Limb bones thin-walled, with hollow or cancellous interior, resembling those of *Chasmatosaurus* spp. but noticeably less robust. Shaft of radius with well defined fossa for origin of deep digital flexors. Femur dorsally arched in distal two thirds, with deep intertrochanteric fossa, and with distinct fourth trochanter situated half-way down shaft. Calcaneum with stepped antero-medial face and posterior tuber.

DESCRIPTION

SKULL: The skull of *Kalisuchus rewanensis* is represented by fragments including a right maxilla (the holotype), a left jugal, a section of skull roof and portions of the mandibles. Evidently these fragments were derived from several animals: they are of disparate sizes and were collected on different occasions.

The maxilla is typically archosaurian in structure (Plate 1, figs. A–C; Plate 2, fig. A). It is cleanly broken at the back but is well preserved elsewhere and shows details of its contacts with lacrimal and premaxilla. The robust tooth-bearing portion is roughly semicircular in cross-section, with a flat medial face, and flares outwards a little beneath the antorbital fenestra. In advance of this the maxilla runs slightly inwards, indicating that the snout was relatively narrow. The lack of maxillary contribution to the palate makes it clear that the internal naris was a long slit adjoining the maxillary tooth row. At the rear of the maxilla a shallow groove in the dorso-lateral surface may have accommodated the anterior tip of the jugal beneath the antorbital fenestra. The anterior limit of the fenestra is defined by a thin ascending process; medial off-setting and inwards arching of this process indicate that the sides of the snout were recessed and overhung by the skull roofing bones. The upper rim of the fenestra was formed by the lacrimal, which met a narrow wedge-shaped facet on the ascending process of the maxilla. The junction between maxilla and premaxilla is extremely unusual: at the front of

the maxilla a dorsal groove received the sub-narial ramus of the premaxilla in normal archosaur fashion, but lateral to this there was a more extensive secondary contact. Anteriorly the tooth-bearing part of the maxilla decreases in height and is drawn out laterally above the tooth row as a thick shelf. The shelf has a grooved outer margin and its upper and lower surfaces are marked with fine longitudinal striations. Evidently there was some complex interdigitation between this maxillary shelf and the premaxilla, with the two combining to form an expanded and hood-like tip to the otherwise narrow snout. The down and forwards slope of the maxillary shelf probably indicates that the intact skull possessed the downcurved premaxillae which are characteristic of proterosuchids in general.

The left jugal is incomplete at front and back but is nevertheless fully archosaurian in appearance (Figs. 1A–B). Its posterior ramus seems deceptively robust in lateral view; in fact it has a cross-section like an inverted L, with a broadly rounded rim between dorsal and lateral faces. A depression in the lateral face of the posterior ramus is the result of crushing, there being no discernible trace of an attachment surface for the quadrato-jugal. The stump of the anterior ramus is a compressed blade with its outer face looking slightly downwards; its medial face bears a shallow groove for the attachment of the ectopterygoid. The dorsal ramus is a stout, tapering and twisted blade which is slightly arched in cross-section (convex forwards) and has its outer face turned to the rear. At its upper end the dorsal ramus has a finely wrinkled surface, suggesting that the upper rim of the orbit carried rugose ornament (as it does in *Chasmatosaurus vanhoepeni*). The gracefully recurved bar between orbit and lateral temporal fenestra was constructed in standard archosaur manner of postorbital overlapping jugal, with the lower edge of the postorbital fitting into a deep slit in the leading edge of the dorsal jugal ramus. This interlocking between postorbital and jugal is apparently the reverse of that in *Chasmatosaurus vanhoepeni*, where the postorbital has been described as 'grooved on the hind surface to receive the dorsal process of the jugal' (Cruikshank 1972, p. 97).^{*} None of the orbital margin has remained intact, though it is clear from the amount of bone between anterior and dorsal branches of the jugal that the ventral rim of the orbit lay somewhat higher than that of the lateral temporal fenestra. Backwards inclination of the dorsal jugal ramus indicates that the orbit was probably triangular or pear-shaped in outline (narrower below). The

central part of the jugal, directly under the dorsal ramus, is thickened into a near-vertical buttress; this is damaged but seems, originally, to have extended into a prominent process on the lower edge of the jugal.

The skull roof is represented by a heavily crushed and plate-like piece of bone (Fig. 1C). Its asymmetry implies that it does not come from the mid-line, and it is tentatively identified as the left nasal with small portions of prefrontal and lacrimal still attached. This section of skull roof would have formed the dorso-lateral region of the snout immediately above the left antorbital fenestra. At the extreme postero-lateral margin of the specimen deep wedge-shaped impressions mark part of the coarsely interdigitating suture with the frontal. Lateral to this the nasal is overlain by a narrow slip of bone identified as part of the left lacrimal and this, in turn, is overlain by a tiny fragment of the left prefrontal. Lacrimal and prefrontal would have defined the antero-dorsal rim of the orbit, though none of this rim is preserved in the specimen. Along its antero-lateral edge the nasal is thickened and grooved for the attachment of the maxilla. Transverse arching of the nasal is very weak and has undoubtedly been reduced by crushing; in the intact skull that arching would have been considerably stronger, marking the break in slope between the roof and the side of the snout.

The mandibles are represented by fragments (Plate 2, fig. C; Plate 3, figs. A–F) identical with counterparts in *Chasmatosaurus vanhoepeni* and *C. yuani* (see Broili and Schroder 1934 and Young 1936 respectively). The forwards extent of the Meckelian canal implies that the splenial reached nearly to the unfused symphysis (Plate 2, fig. C; Plate 3, fig. A). In their anterior regions the mandibles are much deeper than broad, but the articular portion of a right mandible shows complete reversal of those proportions (Plate 3, figs. D–F). This antero-posterior shift in jaw proportions might seem unusual but is, in fact, matched in *Chasmatosaurus* and in crocodylians. The glenoid fossa is saddle-shaped and extends out and forwards at about 45° relative to the jaw axis. Shape and alignment of the fossa indicate that the condyle of the quadrate must have resembled that of *Chasmatosaurus* in its structure and orientation (see Cruikshank 1972, fig. 3a). The

^{*} Cruikshank's work (1972) relegated *Chasmatosaurus* Haughton 1924 to the synonymy of *Proterosuchus* Broom 1903 and employed the latter name throughout. My reasons for using the name *Chasmatosaurus* are explained in the discussion.

retroarticular process is robust, but it does not show the strong upwards curvature seen in *Chasmatosaurus*. In front of the glenoid fossa is a sheet-like portion of an unfused prearticular; this is perforated by a small foramen for transmission of the chorda tympani nerve (Plate 3, fig. E).

DENTITION: Maxillae and dentaries each carried a single marginal row of teeth; it is not known if *Kalisuchus* rivalled *Chasmatosaurus* in possessing premaxillary and palatal teeth. Implantation is subthecodont, according to the precise definition given by Romer (1956, p. 442),

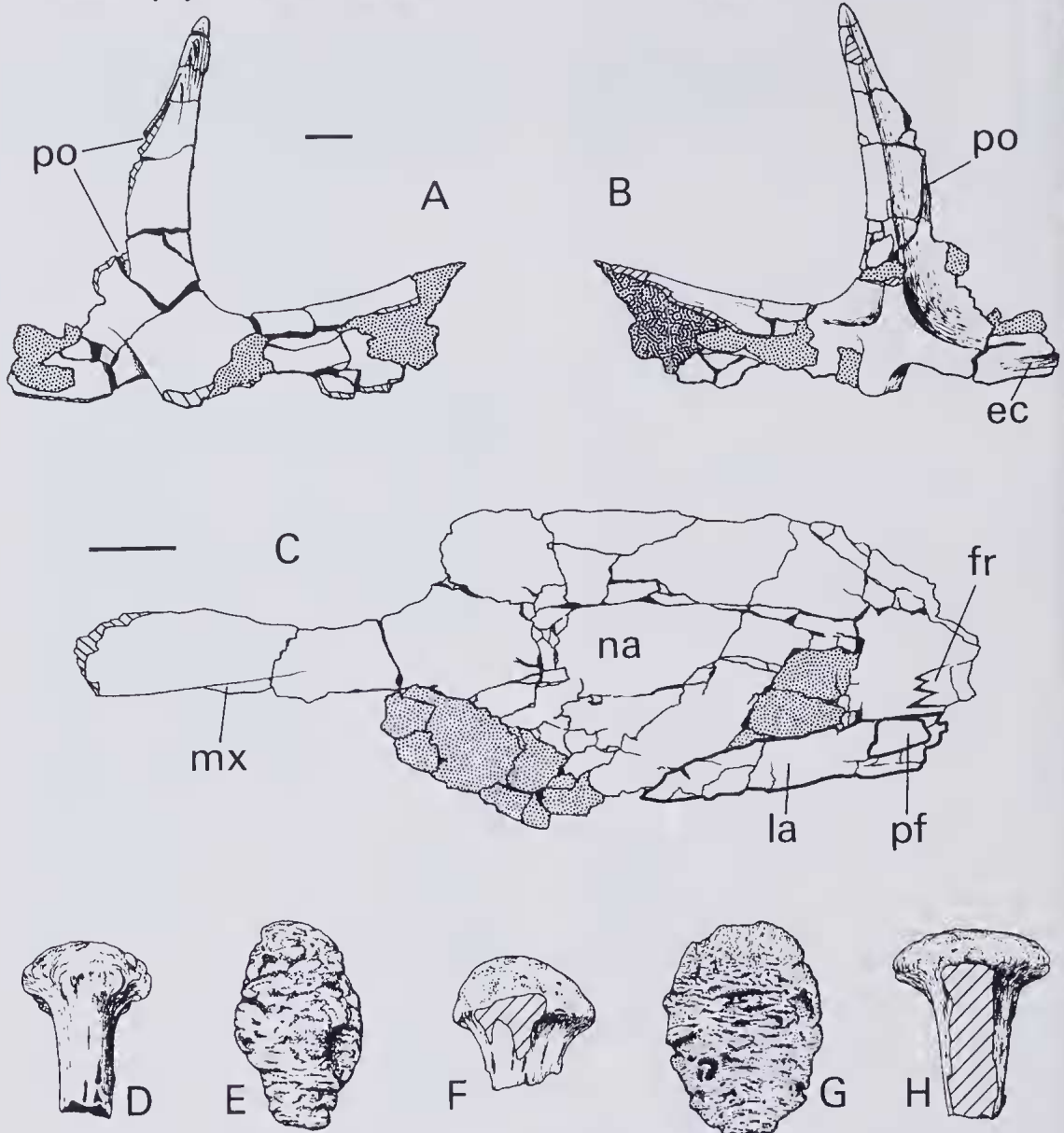


FIG. 1: *Kalisuchus rewanensis* gen. et sp. nov., referred specimens. Each scale indicates 1 cm; matrix indicated by stippling, and broken surfaces by oblique shading. A-B, left jugal (QM F9521) in lateral and medial views, (ec = groove for attachment of ectopterygoid; po = groove for attachment of postorbital). C, crushed section of skull roof (QM F9522) in dorsal view, (fr = impressed area of attachment of frontal; la = portion of left lacrimal; mx = groove for attachment of left maxilla; na = nasal; pf = portion of left prefrontal). D-H, crests of neural spines showing variable development of spine tables, all $\times 1$ (D-E, QM F9523 in posterior (?) and dorsal views; F, QM F9525 in anterior (?) view; G-H, QM F9524 in dorsal and posterior (?) views).

but with the minor distinction that lateral and medial walls of the alveoli are equally high. The medial walls are thin and were apparently very susceptible to breakage (compare fig. C, in Plate 2, with fig. A in Plate 3). Few teeth are preserved in the material, and most of those are broken stumps. The type maxilla contains a near-complete tooth in the fourth alveolus, and a splinter of another tooth is lodged in the sixth and seventh alveoli. The latero-medially compressed, acutely pointed and recurved crowns of the teeth bear a close resemblance to those in *Chasmatosaurus*. The teeth of *C. vanhoepeni* are finely serrated on their rear edges (Gow 1975, p. 117) and so too are those of *Kalisuchus* (Plate 2, fig. B). In addition it is possible that some, or all, of the teeth in *Kalisuchus* were serrated on their leading edges. One replacement tooth has tiny serrations on the leading edge (Plate 2, fig. D); the displaced splinter of tooth in the type maxilla is clearly serrated (Plate 1, fig. B) and its longitudinal convexity implies that it represents a leading edge. The leading edges of the teeth are serrated, in a rather variable pattern, in *C. yuani* (Young 1936, fig. 5) and it seems likely that the teeth of *Kalisuchus* carried similar ornament.

From the limited variation in size of the alveoli it is reasonable to conclude that the dentition was near-isodont. The alveoli are closely packed in linear series and so, of course, were the teeth. In this respect *Kalisuchus* resembled both *C. vanhoepeni* (as figured by Broili and Schroder, 1934) and *C. yuani*. Cruickshank's reconstructions (1972) of *C. vanhoepeni* show decidedly irregular spacing of the teeth, but that irregularity probably stems from the composite nature of the reconstructions. The reconstruction of *C. vanhoepeni* by Broili and Schroder (1934, fig. 4) showed the upper tooth row extending without interruption across the suture between maxilla and premaxilla; but Cruickshank's reconstruction (1972, fig. 3a) shows the hindmost premaxillary teeth distinctly closer to the mid-line than the foremost maxillary teeth and separated from them by a short diastema. The type specimen of *C. yuani* has no diastema; the upper tooth rows diverge as they approach the front of the maxillae and then reconverge in the premaxillae (Young 1936, fig. 1). The arrangement of the upper teeth in *Chasmatosaurus* is either uncertain or variable. But in *Kalisuchus* their arrangement is highly distinctive. In front of its first alveolus the tooth-bearing part of the maxilla is smoothly rounded off (Plate 1, fig. B), implying the presence of a diastema or some other interruption of the tooth row at the junction of maxilla and

premaxilla. The maxillary tooth rows converge towards the front while, at the same time, the maxillae increase in breadth at their anterior ends; this peculiar arrangement indicates that most of the contact between maxilla and premaxilla occurred lateral to the line of the maxillary teeth. It is difficult to escape the conclusion that the premaxillae were transversely expanded; and if the premaxillae did carry marginal teeth the hindmost of these are likely to have been situated outside the line of the maxillary tooth row.

VERTEBRAL COLUMN: The material includes many damaged and isolated vertebrae (most being represented by centra). It is impossible to estimate the vertebral formula, and composite descriptions of neck, trunk and tail vertebrae must suffice. In nearly all respects the vertebrae approach very closely to those of *Chasmatosaurus* (as described by Hughes 1963).

The cervical vertebrae have elongated and spool-shaped centra, each with a prominent ventral keel (Plate 3, figs. G-M). The centra are amphicoelous, having terminal faces which are gently excavated and slightly higher than wide. In some cases the antero-ventral and postero-ventral margins of the centra appear to be bevelled (suggesting the former presence of intercentra), but it is difficult to be certain of this on account of the poor preservation. In anterior neck vertebrae the diapophysis and the parapophysis are situated close together and low down at the anterior end of the centrum (Plate 3, figs. G-I); in succeeding neck vertebrae the rib facets are more widely separated owing to upwards, and slightly backwards, migration of the diapophysis (Plate 3, fig. J). One vertebra from the hindmost part of the neck (or possibly from the foremost region of the trunk) is of considerable interest in that the rib facets of the right side are perfectly preserved (Plate 3, figs. K-M). The parapophysis lies at the antero-ventral margin of the centrum; it is elliptical in outline (with the long axis running forwards and slightly down) and has a raised rim. The diapophysis is situated about half-way up the centrum, but is still close to the anterior margin; it has the outline of a figure 8 (the upper loop being the larger) and also has a raised rim. Duplex construction of the diapophysis clearly indicates the presence of triple-headed ribs in the neck (or anterior trunk) region of *Kalisuchus*.

The dorsal vertebrae are represented by poorly preserved centra (Plate 3, figs. N-O). These are amphicoelous, with terminal faces slightly higher than wide, and are all distinctly shorter than the neck centra. They have weak ventral keels or lack

them entirely. Some broken and dissociated neural spines (Figs. 1D-H) were probably derived from the trunk region (or possibly from the hind part of the neck). They are robust blades of bone, and all have their dorsal edges thickened and expanded into very characteristic spine tables.

The caudal vertebrae (Plate 3, figs. P-R) are very similar indeed to those described and figured for *Chasmatosaurus yuani* by Young (1936).

PECTORAL GIRDLE: Several flat fragments of bone might possibly be portions of the shoulder girdle; that shown in Plate 4, figs. A and B, seems, for example, to be the upper part of a left scapula. None of these fragments can be identified with certainty, and none is well enough preserved to merit detailed description.

FORELIMB: The distal end of a right humerus (Plate 4, figs. C-F) resembles its equivalents in *Chasmatosaurus yuani* and in *C. vanhoepeni* (see Young 1963, fig. 2b, and Cruickshank 1972, figs. 6a-c, respectively). Its relative narrowness (from entepicondyle to ectepicondyle) cannot be regarded as a distinguishing feature and may be largely attributed to damage.

The radius is represented by two examples from the left side, the smaller one being nearly complete. The smaller radius (Plate 4, figs. H-K) is practically identical with that illustrated in *C. yuani* by Young (1936, fig. 9a). It is a slender bone, as it is in *C. yuani*, and is not so stoutly constructed as the radius of *C. vanhoepeni* (see Cruickshank 1972, fig. 6d). The original total length of this smaller radius was probably about 105 mm. The distal section of the second radius (Plate 4, fig. G) is clearly from a much larger animal; when complete this bone probably exceeded 160 mm in length (judging from the proportions of the smaller radius). On both radii the ventro-medial surface of the shaft carries a very distinct fossa for the attachment of the radial head of the deep digital flexors; an identical feature is illustrated by Young (1936) in the radius of *C. yuani*.

PELVIC GIRDLE: The only certainly identified part of the pelvis is the proximal portion of a right pubis (Plate 5, figs. A-B). This fragment consists of a massive buttress culminating proximally in a large facet to meet the pubic peduncle of the ilium. As it is traced distally the buttress curves forwards and down, diminishing in thickness, and becomes drawn out on the medial side into a transverse sheet. This sheet, or pubic apron, is crushed, but is still slightly arched to the front. Its

entire medial margin is damaged, so that it is impossible to determine the extent of the symphysis or of any fenestration. In its general appearance this portion of the pubis resembles its equivalents in pseudosuchians rather than in *Chasmatosaurus*; more specifically, it finds its closest counterparts in *Ornithosuchus longidens* and in *Euparkeria capensis* (see Walker 1964, fig. 11, and Ewer 1965, figs. 11, 12, respectively).

HINDLIMB: The femur is represented by a complete example (Plate 5, figs. C-G) and by two larger proximal ends, all of the left side. The femur is very similar to that of *C. vanhoepeni* (Cruickshank 1972, figs. 9a-d) but is, like the radius, much less robust than in this African form. Cruickshank described the femur of *C. vanhoepeni* as 'almost straight' (1972, p. 108), but the femoral shaft of *Kalisuchus* shows a gentle and very distinctive S-bend (being upwardly arched in the distal two thirds). This curvature can hardly be attributed to post-mortem distortion; wherever the Rewan material has been distorted it has usually been crushed flat. The fourth trochanter is slightly better developed in *Kalisuchus* than in either *C. vanhoepeni* or *C. yuani* (in which latter Young 1963, p. 221, stated that there was 'no clear fourth trochanter'). Both *Kalisuchus* and *C. yuani* have the fourth trochanter situated about half-way down the femoral shaft; in *C. vanhoepeni* it has a more proximal situation.

The two ends of a single left tibia (Plate 5, figs. H-I) are virtually identical with equivalents in *C. yuani* (Young 1936, fig. 11a). So, too, is the distal end of a left fibula (Plate 5, fig. J; compare Young 1936, fig. 11b).

A single left calcaneum is very well preserved and strikingly like that of a crocodylian or of a pseudosuchian in its configuration (Plate 5, figs. K-L). Its antero-medial face is slightly abraded but is clearly 'stepped' to form part of a rotary joint against the astragalus; the postero-dorsal margin has been snapped off (Plate 5, fig. K) but seems originally to have been extended into a definite calcaneal tuber.

DISCUSSION

RELATIONSHIPS OF *KALISUCHUS*

Most Lower Triassic archosaurs are members of the suborder Proterosuchia (as defined by Charig and Reig 1970) and it is likely that the relationships of *Kalisuchus* lie within that taxon. The only well known Lower Triassic archosaur that may not be a proterosuchian is *Euparkeria*

capensis, from the *Cynognathus* Zone of S. Africa (Broom 1913a, b; Ewer 1965; Gow 1970). *Euparkeria* has sometimes been regarded as an advanced proterosuchian that was nearing the pseudosuchian level of organization (e.g. Hughes 1963, Cruickshank 1972) but is best considered as a very primitive pseudosuchian newly descended from proterosuchian ancestry (the traditional view, endorsed by Reig 1970, Charig and Reig 1970). In nearly every feature of its skeletal anatomy *Kalisuchus* is characteristically proterosuchian. Some parts, such as the mandible and the radius, are practically indistinguishable from counterparts in the Chinese *Chasmatosaurus yuani*, while others, such as the femur, are closely matched in the African *C. vanhoepeni*. Still other characters, such as the subtheodont dentition, the triple-headed ribs and (if they are present) the intercentra, are virtually the hallmarks of proterosuchians. In only one or two respects (and notably in its possession of a 'crocodiloid' calcaneum) does *Kalisuchus* resemble pseudosuchians rather than proterosuchians. It is on account of its numerous and detailed resemblances with Chinese and African species of *Chasmatosaurus* that I regard *Kalisuchus* as a proterosuchian, rather than as a very primitive pseudosuchian comparable with *Euparkeria*.

Before attempting to pin down the more immediate relationships of *Kalisuchus* within the Proterosuchia it is necessary to mention two major problems. First there is the fact that the 'only well known genera are *Chasmatosaurus*, *Erythrosuchus* and *Shansisuchus*, and even of these our knowledge is far from complete' (Charig and Reig 1970, p. 140). In consequence it is not possible to make exhaustive comparisons with other proterosuchians; assessments of relationships within the Proterosuchia are, of necessity, very tentative ones. Second, the classification of proterosuchians has long been in a somewhat confused state. Charig and Reig succeeded in unravelling much of the complexity of proterosuchian taxonomy and drew up a useful classification (1970) wherein they recognized two families — the Proterosuchidae (comprising primitive forms) and the Erythrosuchidae (comprising more advanced forms). *Kalisuchus* is strikingly similar to *Chasmatosaurus*, the central genus of the Proterosuchidae, and plainly merits inclusion in the same family.

Within the Proterosuchidae there remains the long-debated possibility that the genus names *Proterosuchus* Broom 1903 and *Chasmatosaurus* Houghton 1924 might be synonyms. The problem of this possible synonymy is very complicated and

has been well summarized, though inconclusively, by Charig and Reig (1970, p. 145 et seq.). More recently Cruickshank (1972) has included the genera *Elaphrosuchus* and *Chasmatosaurus* in the synonymy of *Proterosuchus* and has given a composite account of the latter. The unique type specimen of the genotype (*Proterosuchus fergusi* Broom 1903) had been lost for many years, but was rediscovered and was used by Cruickshank to support his conclusions regarding synonymy. That type specimen, a weathered portion of skull, could be compared with the type specimen of *Chasmatosaurus vanhoepeni* at only one or two points, as was explained by Houghton in 1924. Briefly, Cruickshank has attempted to uphold the synonymy of *Proterosuchus* and *Chasmatosaurus* on the basis of two similarities: in the palatal dentition and in the structure of the ectopterygoids. This is scarcely an overwhelming body of evidence. Moreover, Cruickshank has admitted that the type specimen of *P. fergusi* is less than adequate for comparative purposes (1972, p. 91): 'As the type of *P. fergusi* is such a poor specimen when compared with the other proterosuchians, it is impossible to refer these to the species *fergusi* . . . It is unlikely that any other specimen will ever be assigned to *P. fergusi* in the future'. Apparently the type and only specimen of *P. fergusi* cannot serve as an adequate standard of reference for appraising the status of other specimens. Consequently I regard *P. fergusi* as being of uncertain status and have preferred to employ the very familiar name *Chasmatosaurus* in place of *Proterosuchus*. Recently Charig and Sues expressed a similar opinion (1976, p. 19) and rejected Cruickshank's placing of *Chasmatosaurus* in the synonymy of *Proterosuchus*.

The following classification of proterosuchians agrees in most respects with that recommended by Charig and Reig (1970) and by Charig and Sues (1976). It differs considerably from the classification advanced by Cruickshank in 1972, where *Garjainia* and *Vjushkovia* were regarded as synonyms of *Erythrosuchus*, and where *Euparkeria* was included in the Erythrosuchidae (see discussion by Charig and Sues 1976). In 1972 Romer suggested that the suborder Proterosuchia might be extended to encompass Middle and Upper Triassic thecodontians of the families Prestosuchidae and Proterochampsidae. His reason for including the prestosuchids is unknown; Charig wrote (1976, p. 100) that he could find 'no adequate justification for this extraordinary assignation, nor was Romer himself able to provide one when questioned verbally'. The relationships of the proterochampsids are

uncertain; Reig (1959) and Sill (1967) both favoured crocodylian affinities for *Proterochampsia*, whereas Walker argued (1968) that the animal was a primitive phytosaur. Only Cruickshank (1975) has expressed any agreement with Romer's suggestion that proterochampsids are late-surviving proterosuchians. The following classification agrees with that of Charig and Sues (1976) in excluding prestosuchids and proterochampsids from the Proterosuchia.

SUBORDER PROTOSUCHIA

A. Family Proterosuchidae

Chasmatosaurus. Lower Triassic.⁽¹⁾

C. vanhoepeni Haughton 1924. *Lystrosaurus* Zone, Orange Free State and Cape Province, S. Africa. (Synonyms: ?*Elaphrosuchus rubidgei* Broom 1946; *C. alexanderi* Hoffman 1965.)

C. yuani Young 1936. *Lystrosaurus* Beds, Sinkiang, China.

C. ultimus Young 1964. Ehrmayng Series, SE. Shansi, China. (Type and only specimen originally referred to *C. yuani* by Young in 1958.)

Chasmatosuchus. Lower Triassic.

C. rossicus von Huene 1940. Zone V, northern Russia. (Synonym: ?*C. parvus* von Huene 1940.)

Archosaurus. Upper Permian.

A. rossicus Tatarinov 1960. Zone IV, central European Russia.

Kalisuchus. Lower Triassic.

K. rewanensis. Rewan Formation, SE. Queensland.

B. Family Erythrosuchidae

Erythrosuchus. Lower Triassic.

E. africanus Broom 1905. *Cynognathus* Zone, Cape Province, S. Africa.

Garjainia. Lower Triassic.

G. prima Ochev 1958. Zone V, southern Urals, European Russia.

Vjushkovia. Lower Triassic.

V. triplicostata von Huene 1960. Zone VI, southern Urals, European Russia.

?*V. sinensis* Young 1973. Horizon IV, Sinkiang, China.

Shansisuchus. Lower Triassic.

S. shansisuchus Young 1964. Ehrmayng Series, S.E. Shansi, China.

C. Incertae sedis

Proterosuchus. Lower Triassic.⁽²⁾

P. fergusi Broom 1903. *Lystrosaurus* Zone, Cape Province, S. Africa.

Cuyosuchus. Lower Triassic.

C. huenei Reig 1961. Cacheuta Beds, Mendoza, Argentina.

cf. *Garjainia* (*Chasmatosuchus vjushkovi* Ochev 1961), Zone V, Lower Triassic, southern Urals, European Russia (Tatarinov 1961).

cf. *Chasmatosaurus* (*Ankistrodon indicus* Huxley 1865; *Chasmatosaurus indicus* von Huene 1942), Panchet Group, Lower Triassic, India (Satsangi 1964).

cf. *Erythrosuchus*, Yerrapalli Formation, ? Lower Triassic,⁽³⁾ Godavari Valley, India (Robinson 1967; Chatterjee *et al.* 1969; Chatterjee and Roy Chowdhury 1974).

cf. *Chasmatosaurus*, N'tawere Formation, ? Lower Triassic,⁽⁴⁾ N.E. Zambia (Charig and Reig 1970).

cf. *Chasmatosaurus*, Knocklofty Formation, Lower Triassic, Tasmania (Warren 1972)⁽⁵⁾.

? 'proterosuchian', Yerrapalli Formation, ? Lower Triassic,⁽³⁾ Godavari Valley, India (Cruickshank 1972, p. 118; Charig and Sues 1976, p. 30).

(1) Cruickshank listed a specimen of '?*Proterosuchus*' (1972, table 1) possibly obtained from late Permian sediments (uppermost part of the *Kistecephalus* Zone).

(2) *P. fergusi* came from sediments attributed to the '*Procolophon* Zone', but S. African sediments containing *Procolophon* are probably correlative with those of the *Lystrosaurus* Zone (Kitching 1972 and in Kitching *et al.* 1972).

(3) The upper part of the Yerrapalli Formation is possibly of Middle Triassic age (Jain, Robinson and Roy Chowdhury 1964; Chatterjee and Roy Chowdhury 1974).

(4) The N'tawere Formation may extend into the Middle Triassic (Cox 1969).

(5) Proterosuchian material from the Knocklofty Formation of Tasmania has recently been described (Camp and Banks 1978) and named *Tasmaniosaurus triassicus*. *Tasmaniosaurus* has been referred to the family Proterosuchidae but is clearly not congeneric with *Kalisuchus*.

Of the adequately known and determinate proterosuchians listed above the closest relatives of *Kalisuchus* are *Chasmatosaurus yuani* and *C. vanhoepeni*, from the Lower Triassic of China and S. Africa respectively. Certain parts of the Queensland proterosuchian (notably the limb bones and the mandibles) are nearly identical with counterparts in the Chinese form. The resemblances with *C. vanhoepeni* are a little less striking but are nonetheless very impressive; the limb bones and the vertebrae of *Kalisuchus* have the same basic morphology as those in the African species, but the limb bones are distinctly less robust. While *Kalisuchus* differs from *Chasmatosaurus* in some minor details there are several more important differences which preclude assignment of the Australian material to the genus *Chasmatosaurus*.

First, there is a major difference in the structure of the snout. In having the front part of the maxilla flared outwards into a shelf *Kalisuchus* is unique among proterosuchians. This feature seems to indicate that the tip of the snout was transversely expanded and that much of the contact between maxilla and premaxilla was external to the line of the upper tooth row. In *Chasmatosaurus* the tip of the snout is narrow and the premaxilla meets the maxilla in fairly standard archosaurian fashion.

Second, there are some differences in the jugal. In *Kalisuchus* the interlocking between jugal and postorbital is the reverse of that described in *C. vanhoepeni* by Cruickshank (1972), and the L-shaped cross-section of the posterior ramus is almost equally distinctive (though the reconstructions of *C. vanhoepeni* by Broili and Schroder (1934) hint at a slightly similar development). No other proterosuchian matches *Kalisuchus* in having a projection on the ventral margin of the jugal.

Next, it is likely that the upper tooth row of *Kalisuchus* was disrupted by a gap, or by off-setting, at the junction between maxilla and premaxilla. The upper tooth-row of *C. yuani* is certainly different (Young 1936, fig. 1); the arrangement of the upper teeth in *C. vanhoepeni* is either uncertain or variable (compare illustrations of Broili and Schroder 1934 with those of Cruickshank 1972) but is likely to have differed from that in *Kalisuchus* by virtue of the dissimilarity in snout construction.

The very characteristic spine tables of the *Kalisuchus* vertebrae seem to be much more strongly developed than in any other proterosuchian. No comparable structures are present in *C. yuani* (Young 1936, figs. 6, 7). Spine tables occur,

on the fourth and subsequent neck vertebrae of *C. vanhoepeni*, but Cruickshank described these as 'lateral expansions' and stated that they were lacking from the typical thoracic vertebrae (1972, p.104). All the centra of *Kalisuchus* are amphicoelous, and so, too, are those of *C. yuani*; Cruickshank has ascertained (1972) that the trunk centra of *C. vanhoepeni* are procoelous.

The incompletely known pubis of *Kalisuchus* is broadly comparable in structure with that of *C. vanhoepeni* but seems to be most closely matched in the pseudosuchians *Euparkeria* and *Ornithosuchus*.

Last, the surprisingly 'crocodiloid' calcaneum of *Kalisuchus* is quite unlike that in *C. vanhoepeni* (see Cruickshank 1972, fig. 10, but note the revised identification of ankle bones by Gow 1975, p. 117). In possessing this complex tarsal structure *Kalisuchus* resembles pseudosuchians and crocodilians rather than any of the proterosuchians.

The conclusion that *Kalisuchus* is a close relative of *Chasmatosaurus* derives support from the fundamentally similar build of skeleton and skull. But superimposed upon that near-*Chasmatosaurus* framework of structure is a range of diagnostic differences in skull, dentition, pelvic girdle and limb bones. All those diagnostic differences in *Kalisuchus* may be regarded as advances from the structural conditions in *C. vanhoepeni* (and, to a lesser extent, from those in *C. yuani*); so, too, may the more subtle distinctive features in *Kalisuchus* (such as the more delicate limb bones and the more distal location of the fourth trochanter).

In every distinctive feature of its skull, dentition and postcranial skeleton *Kalisuchus* represents a definite advance on the basic proterosuchid pattern exemplified by *Chasmatosaurus*; and it seems that those advances were headed in the direction of pseudosuchians rather than in the direction of erythrosuchids. Proterosuchids were relatively slender animals that probably resembled crocodiles in outward appearance, but erythrosuchids were massive and stocky creatures that have been likened to hippos (see figs. 3 and 7 in Charig and Sues 1976). Some pseudosuchians retained the crocodile-like body form of the proterosuchids, but many tended to a more gracile, and eventually near-dinosaurian, body plan. The fact that *Kalisuchus* has relatively slender limb bones (by comparison with *C. vanhoepeni*) certainly hints at an approach to the pseudosuchian facies rather than to the erythrosuchid facies. And this suspicion of incipient progress towards pseudosuchians is reinforced by several features of the

skeletal anatomy: the expanded tip to the snout, the rather delicate construction of the pubis, the upwards arching of the femoral shaft, and the 'crocodiloid' morphology of the calcaneum. Those distinctive features of *Kalisuchus* are matched in pseudosuchians of one sort or another, but they are not found in erythrosuchids. *Kalisuchus* also compares favourably with pseudosuchians in having a long neck (with cervical centra longer than wide) and a long tail; in erythrosuchids, both these sections of the vertebral column were shortened and the cervical centra were much wider than long.

To summarize, *Kalisuchus* is a close relative of *Chasmatosaurus*, the best known of proterosuchids, and is perhaps a little more closely related to the Chinese *C. yuani* than to the African *C. vanhoepeni*. The diagnostic differences between *Chasmatosaurus* and *Kalisuchus* testify that the latter is the slightly more advanced form. Nowhere in its skeletal anatomy does *Kalisuchus* show any obvious tendency towards erythrosuchid organization; instead it displays a small, but definite, advance towards pseudosuchians. That small advance is suggestive of a proterosuchid ancestry for pseudosuchians; it does not support the idea of an erythrosuchid ancestry (a widespread view, based on the evidence of *Euparkeria*), but accords fairly well with the suggestion that pseudosuchians evolved from animals transitional between proterosuchids and erythrosuchids (Reig, 1970).

Finally, the relationships of *Kalisuchus* give a useful indication of age for the Rewan Formation. The Rewan fauna is dominated by labyrinthodont amphibians (Bartholomai and Howie 1970; Howie 1972a, b; Warren 1972) but these are of limited value for purposes of dating and correlation. On the evidence of plant fossils Balme concluded (1969) that the Rewan sediments of the Bowen Basin extended from late Permian to early Middle Triassic; that conclusion was incorporated by Anderson and Anderson in their review of Gondwanaland biostratigraphy (1970, chart 21), and Warren showed the Rewan Formation as essentially Lower Triassic in age (1972, table 1). This consensus is reinforced by the presence of *Kalisuchus* in the Rewan fauna, because proterosuchids range from the uppermost Permian to the late Lower Triassic (Charig and Reig 1970, table 2). *Chasmatosaurus* is most abundant near the base of the Lower Triassic, with the majority of specimens having been found in the *Lystrosaurus* Zone or its equivalents. The Chinese *C. ultimus* came from sediments of the Ehrmayng Series (broadly the equivalent of the

Cynognathus Zone) and may be regarded as a late survivor. Other possible occurrences of *Chasmatosaurus* outside the *Lystrosaurus* Zone (or its equivalents) are indicated in the classification given above (p. 20). In short, specimens of *Chasmatosaurus* are nearly all from the *Lystrosaurus* Zone and its equivalents or are, in some questionable cases, from levels immediately above or below; and the great majority of specimens is from the lower part of the *Lystrosaurus* Zone. As *Kalisuchus* is a little more advanced than *C. yuani* and *C. vanhoepeni* it is reasonable to conclude that its parent sediments are equivalent to the upper part of the *Lystrosaurus* Zone (or, possibly, to the lower part of the *Cynognathus* Zone). This tentative correlation is supported by recent studies of plant microfossils; Dr C. B. Foster has informed me (pers. comm.) that assemblages from the basal 120 m of the Rewan Formation in the Theodore-Moura area are closely comparable with those of the lowermost (Maitur) member of the Indian Panchet Group. The basal parts of both the Rewan and the Panchet can be identified with the *Protohaploxypinus reticulatus* Zone (uppermost Permian) of the Sydney Basin, N.S.W.

PALAEOECOLOGY

Kalisuchus, like other proterosuchids, probably resembled a crocodile in outward appearance (see the restorations of *Chasmatosaurus* given by Broili and Schroder 1934, Charig and Sues 1976). The proximal articular surface of the femur is terminal in position, indicating that the thigh was not carried erect, but that *Kalisuchus* was a primitive 'sprawler'. Cruickshank estimated that *Chasmatosaurus vanhoepeni* would not have exceeded 1.5 m in overall length when fully grown (1972, p. 113), but *Kalisuchus* seems to have attained somewhat greater size. Using Cruickshank's illustrations and measurements of *C. vanhoepeni* it is possible to obtain estimates of total body length for several individuals of *Kalisuchus* (Table 1) — on the assumption, of course, that the two animals were roughly comparable in body proportions.

Chasmatosaurus has been envisaged as a rather crocodile-like predator that was equally at home in water and on land (e.g. see Broili and Schroder 1934, Tatarinov 1961, Reig 1970, Cruickshank 1972), and it is likely that *Kalisuchus* led a similar existence. Aside from *Kalisuchus*, the Rewan fauna comprised abundant labyrinthodont amphibians, occasional small reptiles (superficially lizard-like paliguanids, prolacertids and procolophonids), rare lungfishes (represented by

tooth plates), and actinopterygian fishes and molluscs (both represented by fragments preserved in coprolites — see Plate 5, fig. L). Evidently *Kalisuchus* was the dominant predator in the Rewan environment; it presumably exploited the flourishing population of amphibians and might also have supplemented its diet by taking smaller reptiles and fishes.

Several structural adaptations of *Kalisuchus* are clearly those of a predator. The tip of the snout is likely to have been downcurved, though perhaps not to the extent that it was in *Chasmatosaurus*. Such curvature of the snout was probably an adaptation for grasping slippery prey and for reducing the risk of its escape.

The unfused, and seemingly very loose, mandibular symphysis probably allowed some spreading of the mandibles during feeding. Oblique orientation of the glenoid fossae would have caused the mandibles to splay apart as they were depressed; then, as the mouth was closing, left and right mandibles would have been drawn together. Latero-medial spreading and closure of the mandibles was automatic, and it ensured that the lower tooth rows shifted inwards, towards the mid-line, as they bit upwards into the prey. The upwards and inwards bite of the lower teeth would have afforded better purchase on slippery and wriggling prey.

Whether or not the skull of *Chasmatosaurus* was streptostylic is open to debate. Gow argued (1975) that streptostyly would have been possible only when the lower temporal bar had been breached (thus freeing the quadrate from linkage to quadrato-jugal and jugal); but Cruickshank (1972) maintained that quadrate movements were possible by virtue of a sliding contact between jugal and quadrato-jugal. The evidence from *Kalisuchus* is equivocal, but it is noteworthy that the maxilla and the jugal were found isolated and without attached portions of adjoining skull bones.

TABLE 1: ESTIMATES OF TOTAL BODY LENGTH FOR FIVE SPECIMENS OF *KALISUCHUS REWANENSIS*.

Specimen	Total length (m)*
left radius (QM F9541), c. 10.5 cm long	1.89
left radius (QM F9540), c. 17.0 cm long	3.06
left femur (QM F9543), c. 11.8 cm long	1.18
proximal end of left femur (QM F10126), c. 20.5 cm long	2.05
two ends of left tibia (QM F9544), c. 10.5 cm long	1.20

* Estimated using Cruickshank's (1972) data for *Chasmatosaurus (Proterosuchus) vanhoepeni*.

That fact suggests that bones of the upper jaw and cheek regions were loosely connected in *Kalisuchus*. But whether or not those bones were capable of independent movements, and whether or not such movements were passive or voluntary, can only be resolved with the aid of better material. Nevertheless, cranial kinesis, whatever its nature, is characteristic of predators that kill and swallow relatively large prey, and the skull of *Kalisuchus*, with its seemingly loose construction, might well have been a kinetic one.

Other structural adaptations of *Kalisuchus* are less readily explained. First there is the transversely expanded tip to the snout. A somewhat similar structure occurs in another group of thecodontians, the stagonolepidids (or actosaurids), which have been variously regarded as scavengers, carrion-eaters, herbivores or feeders on invertebrates. Walker suggested (1961) that the expanded premaxillae of stagonolepidids were useful for grubbing about in soft vegetation or for digging out invertebrates. But it is difficult to offer any comparable explanation in the case of a predator like *Kalisuchus*; its premaxillae are unknown, and the exact form of the snout remains to be seen.

Next there is the presence of triple-headed ribs in the posterior neck (or anterior trunk) region. There has been considerable debate about which early archosaurs did (or did not) possess triple-headed ribs (Tatarinov 1961, Hughes 1963, Charig and Reig 1970). They seem to have occurred in *Chasmatosaurus*, *Chasmatosuchus*, *Kalisuchus*, *Erythrosuchus*, *Garjainia* and *Vjushkovia* (though not necessarily in every species of polytypic genera). In addition Ewer reported (1965) the occurrence of virtually three-headed ribs in the early pseudosuchian *Euparkia*. Three-headed ribs would have been practically immovable (unless the three heads were arranged in a straight line), and they would effectively have stiffened the region of neck or trunk in which they occurred. In *Kalisuchus* and *Chasmatosaurus* stiffening at the base of the neck might be regarded as an adaptation for a near-crocodilian method of swimming (see Cruickshank 1972, p. 113 and p. 119).

The swollen crests of the neural spines (Fig. 1, D-H) also merit brief comment. These were probably embedded in a dermis of considerable thickness, but they do not seem to have supported any dermal armour (there being no scutes in any of the Rewan material). Lack of dermal armour is apparently a primitive characteristic common to all proterosuchians (except, possibly, the South American *Cuyosuchus*). Thornley (1970) made a

detailed examination of skin remnants preserved in one specimen of *Chasmatosaurus vanhoepeni* and found traces of epidermal structures resembling scales.

The Rewan vertebrate fauna is ecologically distinct from faunas of comparable age in other areas of Gondwanaland. Early Lower Triassic faunas in Africa, India, China and Antarctica are dominated by synapsid reptiles including the very characteristic *Lystrosaurus*. The Rewan fauna has all the constituents of the typical *Lystrosaurus* Zone (or equivalent) assemblage in other continents — *except* synapsids. Instead of being dominated by synapsids the Rewan fauna is dominated by labyrinthodont amphibians, a fact that lends the fauna a decidedly Palaeozoic cast and makes reliable correlation with other Lower Triassic sequences very difficult.

Lystrosaurus was an amphibious herbivore, something like a modern hippo, that thrived in lakes, rivers and marshes in other continents during the early part of the Lower Triassic. Rewan sediments exposed at the Crater represent a fresh-water environment that would seemingly have been an ideal habitat for *Lystrosaurus*. Yet the abundant vertebrate material from the Crater contains no recognizable fragment of any synapsid. Even the broken vertebral centra of *Lystrosaurus* are very characteristic in appearance (e.g. see Colbert 1974, fig. 12) and would not be easily overlooked. In early Triassic times *Lystrosaurus* and its allies were widespread and abundant in most areas of Gondwanaland, so that their absence from the Rewan fauna is very perplexing. It is difficult to explain the absence of synapsids by arguing that the Rewan fauna is earlier or later than Lower Triassic. Palaeobotanical evidence establishes a late Permian age for the base of the Rewan Formation, so that the Crater horizon (which is about the middle of the formation) can scarcely be earlier than Lower Triassic. In any case, it seems unlikely that *Kalisuchus* should ante-date the somewhat less advanced *Chasmatosaurus*. If, on the other hand, the Crater horizon were Middle Triassic one would expect to find few labyrinthodonts, progressive and near-dinosaur thecodontians (rather than a proterosuchian) and, again, synapsids. There seems little doubt that the Rewan fauna from the Crater is Lower Triassic; but I suspect that it is a relict Palaeozoic fauna with a sprinkling of newly-introduced Mesozoic forms (such as *Kalisuchus* and, perhaps, some of the smaller reptiles). Such an explanation would account for the oddly archaic aspect of the fauna and, hence, for the problem of obtaining a

satisfactory estimate of age. Exactly why synapsids such as *Lystrosaurus* had not invaded the Rewan environment remains a mystery; it is not easy to conceive of any barrier that would have permitted passage of one amphibious reptile (*Kalisuchus*) and barred the entry of another (*Lystrosaurus*).

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PLATE I

Kalisuchus rewanensis gen. et sp. nov. Holotype (QM F8998), a right maxilla, in lateral (A), ventral (B), and dorsal (C) views. All $\times 2$.

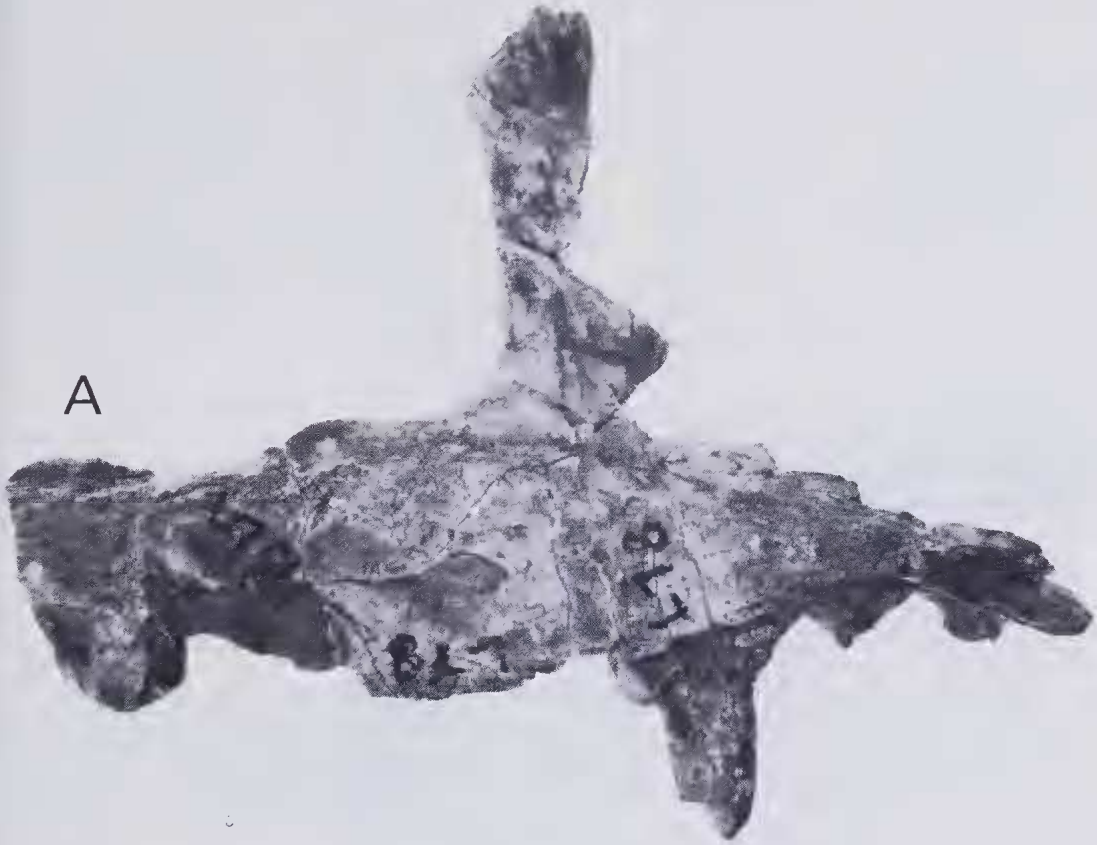


PLATE 2

Kalisuchus rewanensis gen. et sp. nov. Holotype and referred specimen.

FIG. A: holotype, right maxilla (QM F8998), in medial view, $\times 2$.

FIG. B: tooth in 4th alveolus of holotype; in medial view, $\times 6$, to show fine serrations on rear edge.

FIG. C: referred specimen, the symphyseal portion of a right mandible (QM F9526), in medial view, $\times 1$. Note remnants of thin bony walls medial to alveoli.

FIG. D: close-up view ($\times 5.5$) of replacement tooth indicated by arrow in Fig. C; note fine serrations on front edge.

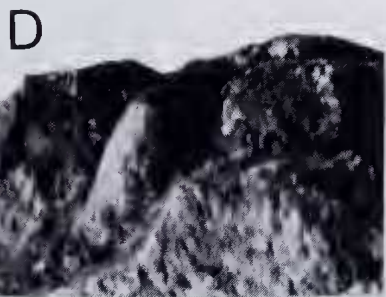
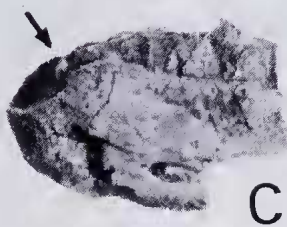
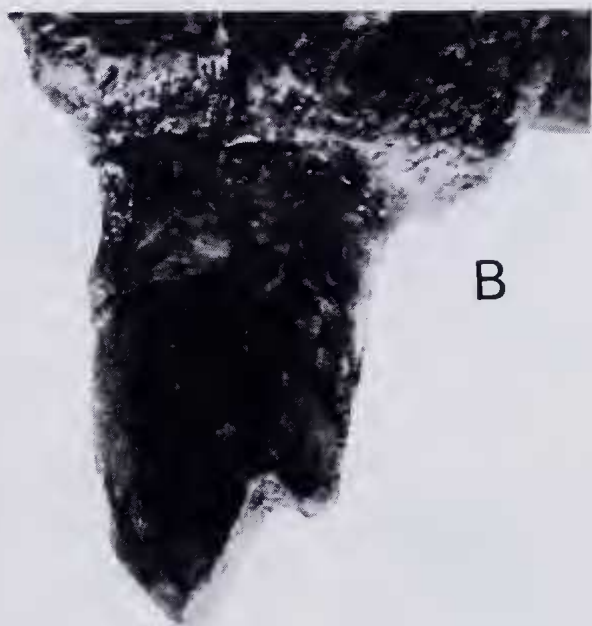
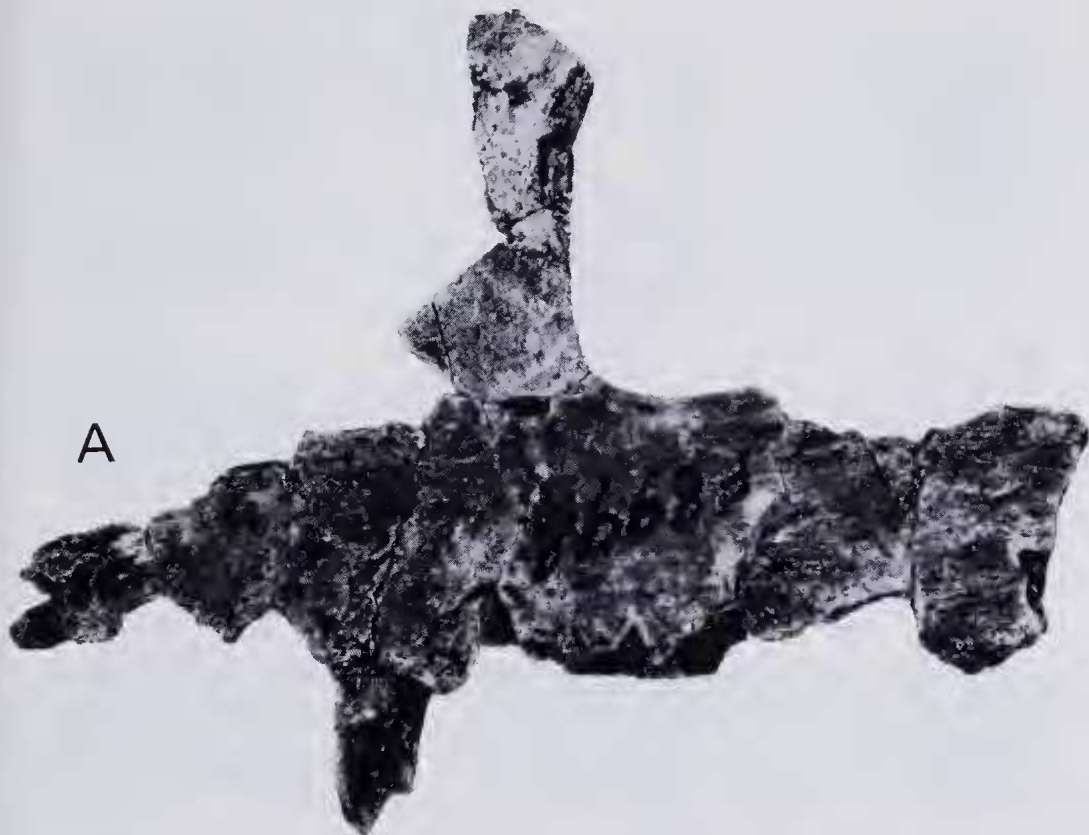


PLATE 3

Kalisuchus rewanensis gen. et sp. nov. Referred specimens. All $\times 1$.

- FIGS. A-C: symphyseal portion of right mandible (QM F9527) in medial (A), dorsal (B) and lateral (C) views.
- FIGS. D-F: articular portion of right mandible (QM F9528) in lateral (D), dorsal (E) and medial (F) views.
- FIG. G: cervical centrum (QM F9529) in anterior view, showing parapophysis and diapophysis close together and low down on anterior rim.
- FIG. H: anterior portion of cervical centrum (QM F9530) in posterior view, showing cancellous interior and strong ventral keel.
- FIG. I: anterior portion of cervical centrum (QM F9531) in posterior view, showing parapophyses, diapophyses, cancellous interior and rather weak ventral keel.
- FIG. J: cervical centrum (QM F9532) in right lateral view, showing slightly abraded parapophysis and diapophysis.
- FIGS. K-M: posterior cervical centrum (QM F9533) in right lateral (K), ventral (L) and anterior (M) views. Areas of rib attachment outlined in ink; note 'figure 8' construction of diapophysis.
- FIGS. N-O: dorsal centrum (QM F9534) in left lateral (N) and ventral (O) views.
- FIG. P: anterior caudal vertebra (QM F9535) in left lateral view; the neural arch is incomplete.
- FIG. Q: mid-caudal centrum (QM F9536) in right lateral view.
- FIG. R: posterior caudal centrum (QM F9537) in left lateral view.

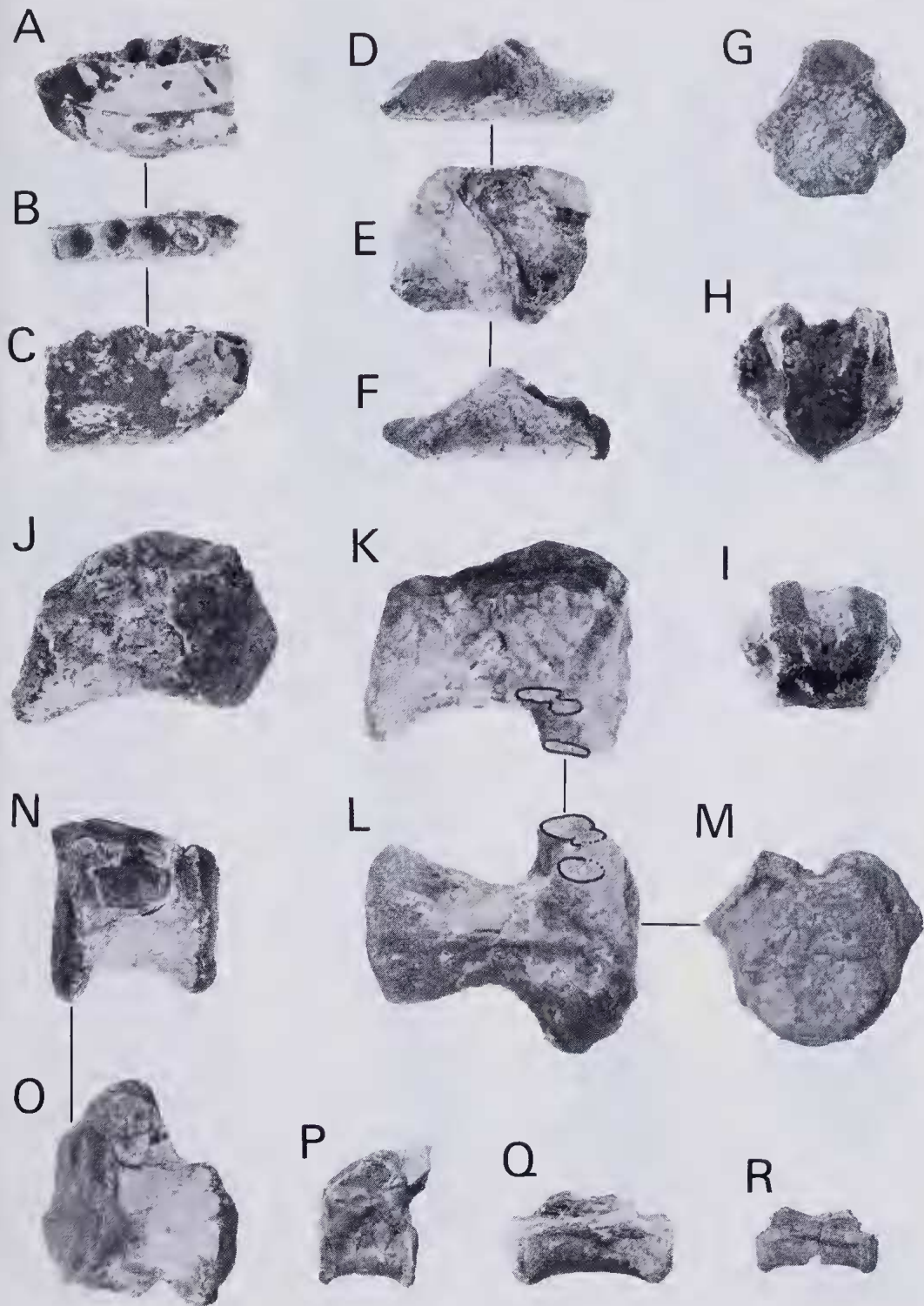


PLATE 4

Kalisuchus rewanensis gen. et sp. nov. Referred specimens. All $\times 1$.

FIGS. A-B: ? upper part of left scapula (QM F9538) in dorsal (A) and lateral (B) views.

FIGS. C-F: distal portion of right humerus (QM F9539) in proximal (C), dorsal (D), ventral (E) and distal (F) views.

FIG. G: distal portion of left radius (QM F9540) in medial view, showing fossa for attachment of deep digital flexors.

FIGS. H-K: left radius (QM F9541) in anterior (H), medial (I), proximal (J) and distal (K) views; part of proximal articular surface is preserved, but distal end is lacking.

FIG. L: coprolite from the Crater (QM F9547), possibly attributable to *K. rewanensis*.

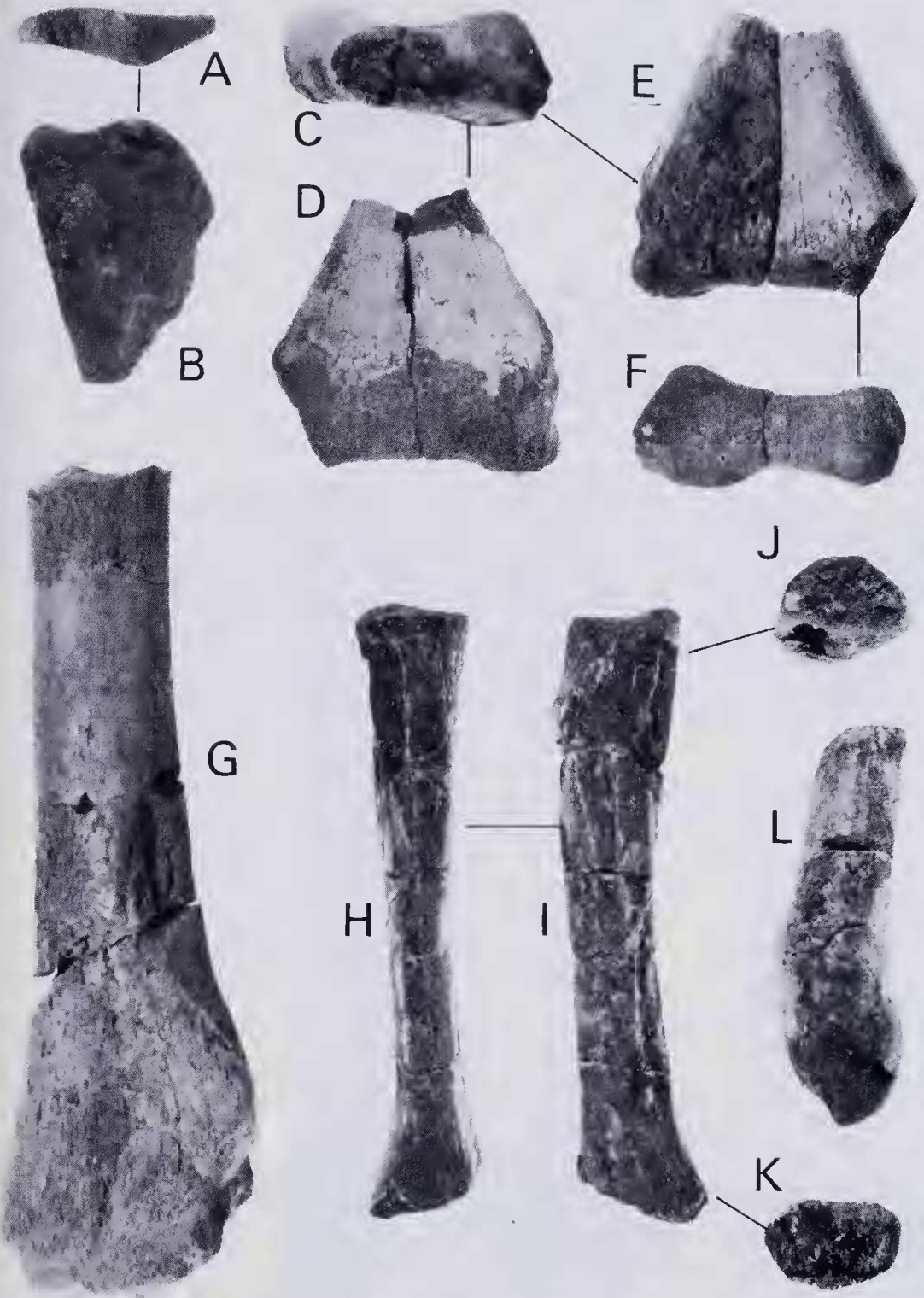


PLATE 5

Kalisuchus rewanensis gen. et sp. nov. Referred specimens. All $\times 1$.

FIGS. A-B: proximal portion of right pubis (QM F9542) in antero-medial (A) and postero-lateral (B) views.

FIGS. C-G: left femur (QM F9543) in ventral (C), anterior (D), dorsal (E), proximal (F) and distal (G) views.

FIGS. H-I: proximal (H) and distal (I) ends of a single left tibia (QM F9544) in anterior view; a considerable portion of the shaft is missing.

FIG. J: distal portion of left fibula (QM F9545) in medial view.

FIGS. K-L: left calcaneum (QM F9546) in proximal (K) and distal (L) views.



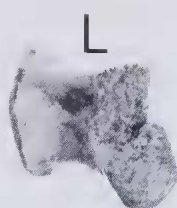
A



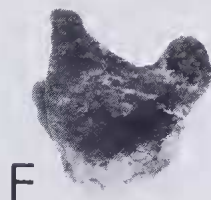
B



K



L



F



J



C



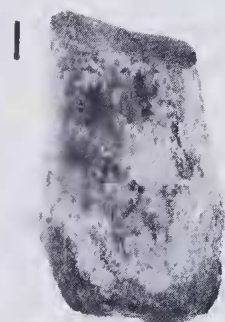
D



E



H



I



G